

Retention around and long-distance dispersal between oceanic islands by planktonic larvae of benthic gastropod Mollusca

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Abstract: Indo-Pacific species of gastropod mollusks often have very wide geographic distributions sometimes extending halfway around the world, from the Marquesas or Hawaiian Islands westward throughout the tropical Pacific and Indian Oceans to the Red Sea and eastern African coast. For a gastropod species to attain such a wide distribution and yet also maintain genetic continuity among so large a number of disjunct populations, some sort of dispersal must occur among the many scattered oceanic islands within the species range. One way this can be accomplished is by long-distance dispersal of planktonic larvae. It is proposed that a small fraction of the total veligers produced by a gastropod species on any particular oceanic island, such as the island of Hawaii, will escape the effect of local circulation and as a consequence will have the possibility to be passively transported by oceanic currents to other remote islands. Evidence from plankton tows taken in proximity to Hawaii, when related to a knowledge of local mesoscale circulation, shows how larvae can be dispersed outside the influence of local island circulation. At the same time, plankton samples from the tropical central and western Pacific Ocean reveal how gastropod veligers are passively advected over long distances by ocean currents. Furthermore, drift bottle data illustrate how gastropod veligers, once entrained within the North Equatorial Current, can encounter other oceanic islands and give evidence for the probability of such an island encounter.

Notwithstanding evidence that larvae can be dispersed away from their native island (in this instance from the island of Hawaii), it is inferred that gastropod species are largely self-sustained by veligers from indigenous populations. For such recruitment from local populations to occur, veligers must (1) be constrained by the local hydrography to remain within the proximity of their natal island, (2) survive the vicissitudes of planktonic life in sufficient numbers and complete development to the competent stage when settlement and metamorphosis become possible, and (3) must be returned passively to a suitable sublittoral environment by the local circulation. Evidence from plankton tows, a knowledge of mesoscale circulation, and data from drift-bottle returns allow an explanation of how larvae can be retained and how they are ultimately returned to their island of origin. Paradoxically, it seems that the hydrological phenomena that sometimes return larvae to their natal island can, in other instances, passively transport veliger larvae out to sea.

Oceanic islands, because of their spatial isolation and as a consequence of their volcanic origin from the floor of the ocean, present unusual opportunities for the study of dispersal and its biogeographic and evolutionary consequences (Clague and Dalrymple, 1989; Walker, 1990). A number of questions immediately arise. Are marine invertebrates on isolated oceanic islands mostly endemic species or are such islands inhabited predominantly by very widely distributed species? How are oceanic islands initially populated? How do island populations once established maintain themselves in apparent isolation? Can island populations maintain themselves principally by the recruitment of their own larvae?

An insight into the distributional patterns found among marine gastropod mollusks on oceanic islands can be gained by considering the family Architectonicidae. Bieler (1993) has shown that the geographic range of *Psilaxis radiatus* (Röding, 1798) encompasses oceanic

islands throughout the tropical Pacific from the Marquesas and Hawaiian Islands westward to the Indian Ocean and eastern Africa and northwestward into the Red Sea (Fig. 1). Among the 20 species of Architectonicidae known to occur on the Hawaiian Islands, three-fourths have geographic ranges very similar to that of *P. radiatus*, extending almost halfway around the world. Such very wide geographic distributions among contemporary Indo-Pacific species can only be explained by some form of long-distance dispersal (Scheltema 1989, 1992).

The Architectonicidae are not an isolated example. The Cypraeidae (cowries) also are widely distributed throughout the Indo-Pacific. Among the 16 Holocene Indo-Pacific genera enumerated by Kay (1995: 218; table 1), 15 are known to include species with planktonic larvae. Schilder (1969) listed 11 species from Hawaii among which eight are known also from eastern Africa. Indeed, some Cypraeidae that occur in the Indian Ocean and tropi-

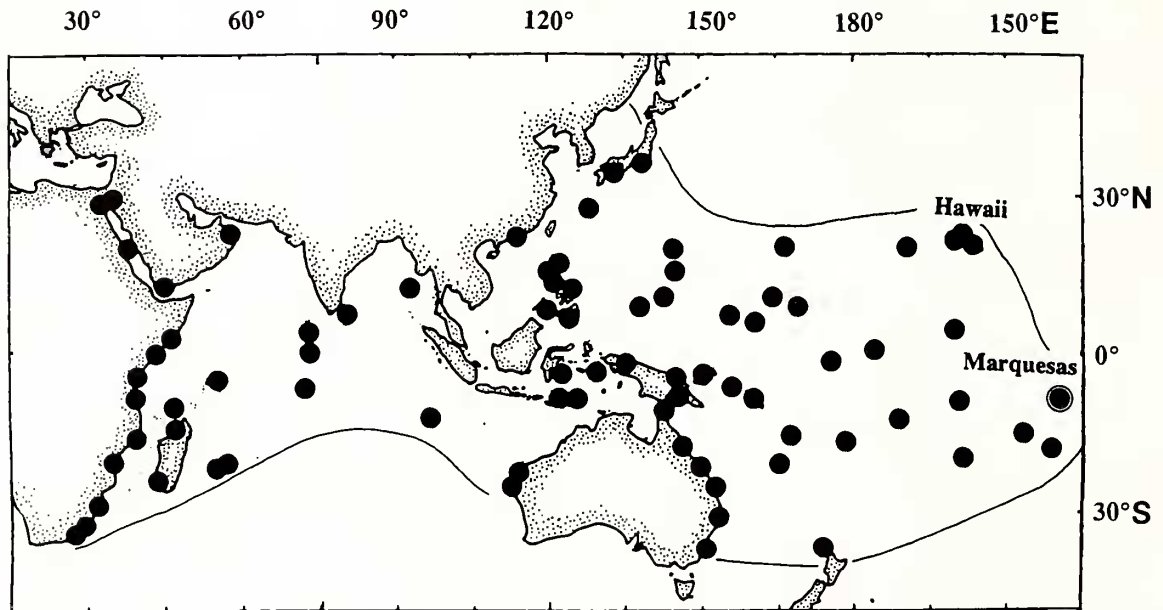


Fig. 1. Geographic distribution of *Psilaxis radiatus* (Architectonicidae). The species range extends from the Marquesas (encircled point) to eastern Africa and the Red Sea. Two additional locations in the eastern Pacific not shown are considered by Bieler to be from non-reproducing, expatriot populations. The continuous line delimits the approximate range of the species. (Modified after Bieler, 1993).

cal western and central Pacific are known also from the eastern Pacific having successfully breached the "eastern Pacific barrier." Emerson and Chaney (1995) have shown that among the 24 eastern Pacific cypraeid species representing eight genera, 15 also are known from the Indo-Pacific. Eight among these 15 amphi-Pacific species are found not only upon eastern Pacific islands (*i. e.* Clipperton, Revillagigedo, Cocos, and Galápagos) but also on the continental shores of central and tropical South America. Some other gastropod families also known to include species with similarly wide geographic distributions throughout the Indo-Pacific region are the Ranellidae (*e. g.* *Cymatium nicobaricum* Röding, 1798), the Coralliophilidae [*e. g.* *Quoyula mondata* (Blainville, 1882)], and the Naticidae (*e. g.* *Natica marochiensis* Gmelin, 1781). Examples given here are but a few specific instances of gastropod species that have large geographic ranges and occur commonly on widely scattered tropical islands.

If indeed oceanic islands are inhabited mostly by broadly distributed species, this fact should be reflected by a low percentage of species endemism. A few examples can be considered here. In waters of the Hawaiian Islands, among the most isolated of central Pacific archipelagos, only 19% of all marine gastropods are endemic. Moreover, among the non-endemic species most are Indo-Pacific (66% of the total) while the remainder (15% of total) are Pacific "Plate" species. Paulay (1989) encountered on remote Pitcairn Island (25°S, 130°W) an attenuated Indo-

West-Pacific marine gastropod fauna with only 2% endemism. Likewise, Kay (1971) found on Line Island (directly in the path of the North Equatorial Current) an endemism of about 2%. Such low endemism is in sharp contrast with land snails which lack an effective mode of regular dispersal and among which endemism can exceed 90% (Kay and Palumbi, 1987).

The extraordinarily large geographic range illustrated by the examples offered above along with the correspondingly low endemism encountered on oceanic islands argues for the hypothesis that long-distance dispersal must be commonplace among tropical sublittoral gastropods and that the initial colonization as well as genetic continuity among marine gastropods must be maintained largely by long-distance dispersal, presumably by the dispersal of teleplanic larvae.

Contemplate now the other side of the problem. How are populations of oceanic islands maintained? Are they self-sufficient and, if so, how is this accomplished? The answer necessarily must take into account the role of passively dispersed larvae, but in this instance instead of being transported away, there must be instead a way to retain larvae over the period of their development and subsequently to return them to their natal island. But how can some larvae be carried away while at the same time others are retained and returned to their native island? It is the purpose of this paper to explain this seeming paradox.

METHODS

The distribution of teleplanic gastropod veligers in open waters of the tropical Pacific Ocean was determined from examination of 328 oblique plankton tows among which 174 were from collections of the Scripps Institution of Oceanography (SIO) obtained during various expeditions over a period of 26 years (see Scheltema, 1986: 243 for a detailed list of expeditions and stations). The remaining 154 samples were 20-min oblique tows to ca. 150 m taken at 1.5-2.5 knots with a 0.75-m net having ca. 0.3-mm mesh. Included were samples from the following expeditions: KNORR, voyage 73 (1979), New Zealand to Hawaii, 36 samples; the Papatua Expedition (1985), Manzanillo, Mexico, to American Samoa, 33 samples; the Helios Expedition (1987), San Diego, Gambier Islands, Pitcairn Island, Austral Islands, and Tahiti (Society Islands), 50 samples; Hydros Expedition (1989), tropical waters between San Diego and Juan Fernández Islands, 35 samples. The samples were reduced to a volume of 0.5-1.0 l, depending on the density of organisms, in 5% formalin with sodium borate added. On the Helios and Hydros Expeditions, all invertebrate larvae were sorted to family at sea. Gastropod veligers were separated and preserved in 80% alcohol with sodium borate added to control pH.

The locations of sampling stations along the western

coast of the island of Hawaii were determined by the hydrography at the time of the study. Plankton tows were taken at night (2240-0530 hrs) between July 23 and 26, 1982, at 1-1.5 knots. The samples were inspected in the laboratory and all veliger larvae removed. Current velocity and direction were determined by radio-tracked Lagrangian drifters. Vertical temperature profiles were determined by expendable bathythermographs (XBT) (see Lobel and Robinson, 1986, 1988, for further details).

RESULTS AND DISCUSSION

Long-distance dispersal

Can long-distance transport of planktonic larvae explain the observed geographic distribution of gastropod species among oceanic islands? What evidence is needed to infer that long-distance larval dispersal occurs? First, it must be shown that planktonic larvae are actually found far out at sea drifting passively with ocean currents. Two examples will suffice to show that larvae indeed do occur in the major ocean currents. Inasmuch as most members of the family Architectonicidae already have been shown to be widely distributed geographically, it is not too surprising to learn that veligers belonging to species of this family are

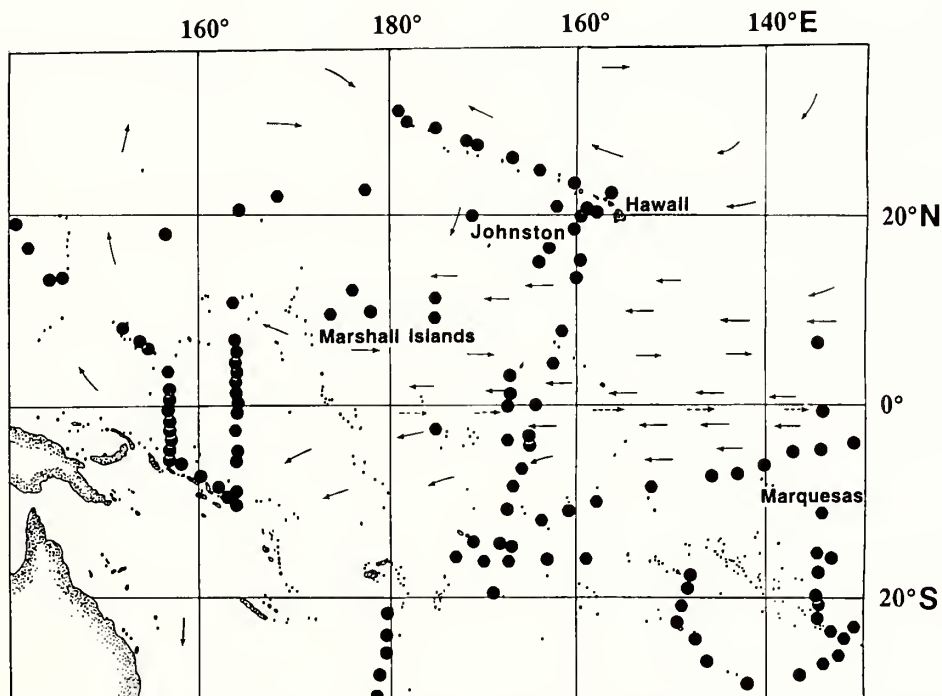


Fig. 2. Distribution of veliger larvae belonging to the gastropod family Architectonicidae from plankton samples taken between the surface and ca. 150 m in the tropical Pacific Ocean using a 3/4 - m net with 0.3 mm mesh (see Scheltema and Williams, 1983).

frequently encountered in the tropical Pacific Ocean (Fig. 2). Likewise, larvae of cypraeid species also have been found distributed over large areas of the central Pacific (Fig. 3).

Second, to approximate the distance that larvae can be advected by an ocean current it is necessary to know the minimum time required to attain competence to metamorphose. There is, however, a paucity of observations on the life histories of tropical Pacific gastropods owing to the difficulty encountered in rearing them in the laboratory. Although teleplanic larvae have a long development as can be inferred from their position of capture in the plankton (Scheltema, 1971, 1992, 1995), the maximum length they are able to delay metamorphosis is usually not known. Govan (1994: 55) estimated that among several species of Pacific *Cymatium*, three months is required to reach competence to settle, but to this must be added the potential for delay of metamorphosis in the absence of a cue for settlement.

Mitton *et al.* (1989) questioned whether gastropod veligers can retain their ability to metamorphose for long periods of time after attaining competence. Evidence from laboratory experiments has shown that certain prosobranch gastropod species can delay settlement long after attaining the competence to metamorphose and that in the absence of a suitable cue can delay settlement and increase two- to

three-fold the length of their planktonic life (Scheltema, 1956, 1961). The opisthobranch *Aplysia juliana* Quoy and Gaimard, 1832, has been shown in the laboratory to delay settlement and metamorphosis up to 300 days (Kempf, 1981). Evidence from larvae taken far out at sea and held in the laboratory confirm that larvae can retain their ability to metamorphose (Scheltema, 1986: 242). Combined evidence from field and laboratory observations provide estimates of the possible delay in settlement of ten species of teleplanic gastropod veligers that range between 30 and 138 days giving a total pelagic life of 55-320 days (Scheltema, 1971).

Third, it is necessary to know the direction and velocity of the major ocean currents likely to passively disperse gastropod larvae. The general circulation of the tropical Pacific is now fairly well known (*e. g.* Tomczak and Godfrey, 1994). Flowing from east to west are the north and south equatorial currents. Between these two westerly moving currents is a seasonally occurring west to east equatorial countercurrent prominent during the summer but much reduced or entirely absent during some winter months (Wyrki, 1966; Toole *et al.*, 1988). There is in addition an equatorial undercurrent flowing toward the east between 50 and 100 m depth at a temperature between 20° and 25°C, sufficient for survival of tropical veliger larvae (Knauss, 1970). The velocities of the major equatorial Pacific surface currents generally fall between 25 and 90 cm/sec but can be

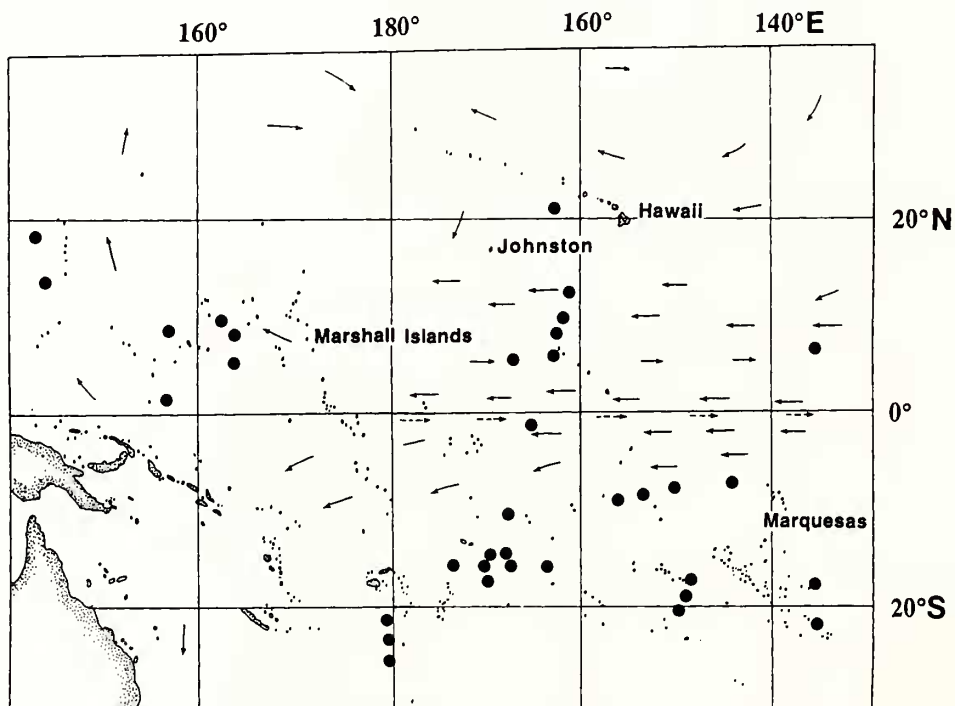


Fig. 3. Distribution of veliger larvae of the gastropod family Cypraeidae from plankton samples taken between the surface and ca. 150 m in the tropical Pacific Ocean (samples as in Fig. 2).

as high as 125 cm/sec in the equatorial undercurrent. Advection by ocean currents provides quasi-permanent or seasonally reoccurring corridors for the passive transport of planktonic veliger larvae and will largely limit the direction and velocity of larval dispersal. Smaller scale details can add some complexity (McNally *et al.*, 1983) but will not substantially alter the major direction of dispersal. Larvae can be readily transported eastward or westward but not northward or southward across the equatorial region except periodically during the time of El Niño (see Richmond, 1990).

If one assumes minimum and maximum current velocities between 25 cm/sec and 125 cm/sec, then in three months [the time required for a *Cymatium* species to attain competence to settle (Govan, 1994)], the median distance a larva can be transported is about 6000 km. This value assumes a straight trajectory, which is unlikely, but gives at least an estimate of the possible magnitude of larval dispersal, even when no delay in metamorphosis is assumed. Under favorable conditions larvae readily could be dispersed for much greater distances.

But what is the probability that a larva will actually encounter another island? Obviously, because it is not possible to follow an individual larva for thousands of kilometers, no direct answer is possible but reasonable inferences can be made from drift-bottle data. The release of 980 bottles made directly within the north and south equatorial currents between 175° and 192° E longitude resulted in a 2.9% recovery. All returns were from islands in the western Pacific including the Solomons, New Guinea, the Carolines, and Gilberts (Scheltema, 1986, from data of Barkley *et al.*, 1964). When bottles released in the central Pacific outside the major east-west currents were included (a total of 2127 bottles) then the percentage of recovery dropped to 1.3%.

Drift-bottle data can provide a "drift coefficient," *i. e.* the likelihood that a passively drifting larva in the open sea will ultimately encounter another island. The probability that the offspring from any particular female will actually be dispersed to another island will depend also upon (1) the fecundity of the individual which will vary both with the species and size of the individual, and (2) the survival of the larvae during dispersal.

Published estimates of fecundity among tropical gastropods are rare. It has been estimated that an egg mass of the architectonicid *Heliacus variegatus* (Gmelin, 1791) contains 30,000 embryos (Bieler, 1993), but it is not known how many egg masses are produced by one female. Some species of Cypraeidae can produce up to 500,000 veligers from a single egg mass (Emerson and Chaney, 1995: 15). Estimates of fecundity of several species of *Cymatium* range from a minimum of 100,000 to over one million eggs per female (Govan, 1994).

Consider now an individual female with one-half million gametes. Even if one uses conservative values, *e. g.* a drift coefficient of 0.013 and assumes a survival of 0.1%, there is a likelihood that at least some larvae (ca. 6) will reach another island (see Scheltema, 1978, 1986, for further details). However, if in its lifetime an individual survives to reproduce more than once, there is the possibility that more than one-half million eggs will be produced. Moreover, if the entire population of an island is considered, the chances that some larvae will be dispersed and encounter another island will increase accordingly.

Larval distribution from plankton samples and calculations based on drift coefficients and known current velocities allow the conclusion that islands within the proximity of major ocean currents will regularly encounter a small but more-or-less continuous flux of larvae, probably sufficient to maintain genetic continuity between islands (see Lewontin, 1974: 213). It is not, however, nearly so evident how larvae could reach some of the more remote oceanic islands not directly in a major ocean current.

Retention of larvae around islands

Consider now the converse question, *viz.* how are populations of gastropods sustained on oceanic islands? To address this problem once again it is necessary to consider surface currents and their effect upon the spatial disposition of planktonic larvae. The island of Hawaii will serve as an example.

Sea surface to the lee of the island of Hawaii is dominated by eddies varying considerably in size, number, and location (Patzert, 1969). Such eddies can be nearly circular or elliptical, and range between 50 and 150 km in diameter. They are predominantly cyclonic, *i. e.* rotating in a counterclockwise direction, driven by the prevailing northeasterly and easterly winds that blow through the restricted passage between the islands of Maui and Hawaii. Although there are some seasonal differences in wind direction and velocity (Blumenstock and Price, 1994: 101, table 4), being more persistently from the north-northeast to east and at greater velocity during the summer months, nevertheless, eddies have been observed in all seasons of the year (Patzert, 1969: table 1).

The eddies can be located either by drogues, inferred from temperature distribution, or derived from the dynamic topography determined by standard oceanographic methods (Fig. 4). The formation of an eddy could require from "approximately two weeks for a weak eddy to a month for a more intense eddy" (Patzert, 1969: 45) and during its lifetime of three or more months it may move up to 350 km in a westerly or northwesterly direction at an average rate of 5.2 km/day, increasing in size as it moves out to sea where finally it is completely dissipated. This lat-

ter process is still poorly understood and was discussed in more detail by Patzert (1969).

The rotation rate of the eddy is related inversely to the depth of the 20°C isotherm and hence the pressure gradient which determines the current velocity and hence the rate of rotation. When the 20°C isotherm is at 70 m depth, the rate of rotation is approximately 3.5 to 4.5 days; when the 20°C isotherm is at about half this depth (30-40 m), the rate of rotation is approximately doubled, to 6 or 7 days (see Patzert, 1969: 14, table 4).

How will such eddies affect the distribution of larvae and their retention around islands? One outcome can be that veligers become entrained and thereby gain time to complete their development to the competent stage when settlement and metamorphosis becomes possible. But does this actually happen? Are gastropod larvae actually entrained in mesoscale eddies? Some initial evidence comes from a series of plankton tows taken between July 23 and 26, 1982, in an eddy off Keahole Point, Hawaii (Fig. 5).

Samples from five different locations within an eddy, including three from its center and two near its edge and taken from the depth of the 24°C isotherm, contained a variety of invertebrate larvae, among them veligers repre-

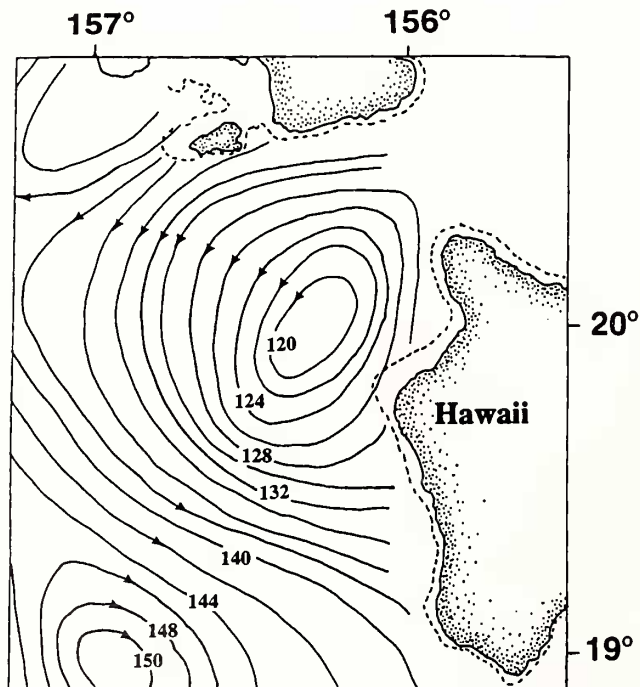


Fig. 4. Dynamic topography (0/500 db) off the Kona Coast of the island of Hawaii in May 1965, to illustrate a large cyclonic eddy. Note also smaller anticyclonic eddies (modified after Patzert, 1969: fig. 12). The eastern edge of the large cyclonic eddy intersects the shoreline on the Kona Coast and could carry gastropod veligers back to their parent populations.

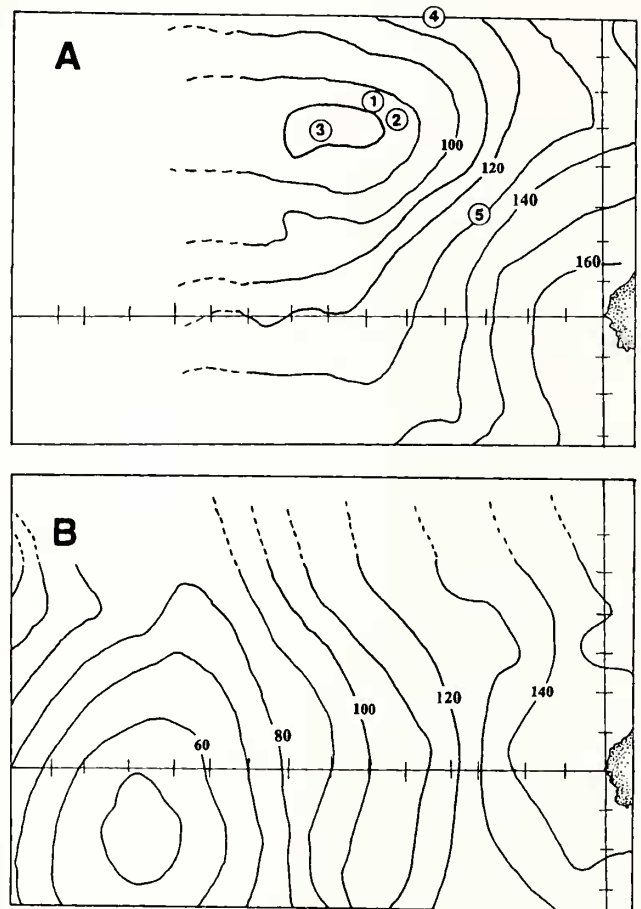


Fig. 5. Cyclonic eddy, Keahole Point, off the western shore of Hawaii during July as defined by the depth of the 20°C isotherm. Contour intervals are 10 m; intervals along scale are 7 km. A. Eddy during July. Plankton sampling locations are indicated by circled numerals. B. Same eddy in September (modified after Lobel and Robinson, 1986: fig. 3). Locations 1, 2, and 3 are at the center of the eddy (see Table 1); locations 4 and 5 are at the outer edge. Samples were taken at night using a 1-m net with 0.5-mm mesh (see Lobel and Robinson, 1986: 492 for details).

sents 12 gastropod families (Table 1) and including teleplanic species found in the open ocean, *e. g.* *Psilaxis radiatus* (Architectonicidae); *Cypraea isabella* Linné, 1758 (Cypraeidae); *Natica gualteriana* Recluz, 1844 (Naticidae); *Carinapex minutissima* (Garrett, 1873) (Turridae); and *Strombus maculatus* Sowerby, 1842 (Strombidae). Larvae are reported here (Table 1) only to family because at present many individuals cannot be reliably identified to species (but see Taylor, 1975). Nonetheless, most specimens are readily recognized to belong to taxa commonly found among the teleplanos.

What will happen to the larvae entrained in an eddy? How will their residence within the eddy affect their retention and possible recruitment to the island of the parent population? Two possible outcomes are proposed. One

Table 1. Families of Gastropoda represented in samples from a mesoscale eddy off the island of Hawaii, July 23-26, 1982 (station numbers refer to positions indicated on chart, Fig. 5)*.

	Eddy Center			Edge of Eddy	
	1	2	3	4	5
Architectonicidae	X	X	X	X	X
Columbellidae		X	X	X	X
Conidae				X	
Coralliophilidae	X	X	X	X	X
Cypraeidae	X	X	X	X	X
Lamellariidae	X	X	X	X	X
Naticidae	X	X	X	X	X
Ranellidae	X	X	X	X	X
Thaididae	X	X	X	X	X
Strombidae	X	X	X	X	X
Triphoridae				X	X
Turridae	X	X	X	X	X
Unidentified	X	X	X	X	X

* Station 1 - July 23, 20° 00.5' N, 156° 25' W
 Station 2 - July 24, 20° 09.5' N, 156° 19.5' W
 Station 3 - July 24, 20° 00' N, 156° 23.5' W
 Station 4 - July 25, 19° 51.5' N, 156° 15' W
 Station 5 - July 26, 19° 51.5' N, 156° 15.5' W

alternative is that veliger larvae are returned to their natal island when the periphery of an eddy intersects the region between 200 m and the shoreline (Lobel, 1989). The anticyclonic eddy along the Kona Coast shown in Fig. 4 illustrates how the usually intermittent and oscillatory tidal current that occurs along the coast is replaced by a strong northerly along-shore current (*i. e.* the eastern edge of the eddy) that could return larvae back to their parent population. Indeed, such currents have been demonstrated empirically by moored current meters (*e. g.* see Robinson and Lobel, 1985).

Return of larvae to the Kona Coast will be determined by (1) the rotation rate of an eddy which has been observed to vary between 4 and 8 days (Patzert, 1969), and (2) the time required for a larva to complete development and gain competence to settle. Consequently, so long as the eddy remains more-or-less stationary and its edge intersects the Kona coastline (Fig. 4) every fourth day of rotation a larva will have the possibility to settle in response to a cue from the bottom. Consequently, larvae with short development times will have ample opportunity to settle along the coast. On the other hand larvae with long development times, for example species of *Cymatium* with a development of three months, could be retained near the island going through numerous rotations of the eddy before they can settle and metamorphose. Rotation of the mesoscale eddy is such that under favorable circumstances both rapidly and slowly developing larvae can be retained and returned to the coastal environment.

A second alternative is that larvae, instead of returning to their natal island, are carried along as the eddy moves out to sea. This seems to have happened to the larvae in the eddy sampled by us off the Kona Coast (Fig. 5). On the upper chart (A) the position of the eddy is shown at the end of July when the plankton tows were taken; the lower chart (B) shows the same eddy in September; it had enlarged between July and September and was moving westward. It may be inferred that most of the entrained larvae were carried out to sea and with the ultimate decay of the eddy these veligers were released to be dispersed subsequently in a generally westward direction by surface currents. The destinies of such ocean-bound veligers are determined by the velocity and direction of the ocean surface currents into which they are "released" and upon their ability to delay metamorphosis until by chance they should encounter some distant island.

Yet, other evidence in support of the hypothesis that larvae can be retained and returned to their natal population comes, as with long-distance dispersal, from the release and recovery of drift bottles. Barkley *et al.* (1964) released more than 4000 drift bottles during 1962, mostly in the region bounded by 18° to 23° N and 154° to 161° W, that is, the area surrounding the major islands of the Hawaiian chain. Recoveries from this experiment show bottles released in proximity to an island will tend to be recovered subsequently on the shore of nearby islands (Table 2; Fig. 6). There were seasonal differences in the percent recovery, the highest (12.5%) occurring between March and May. At other times of the year many fewer bottles were returned, between 2.7 and 6.0%. Even so, the mean annual recovery, 5.5%, was remarkably high for this kind of study. If it is assumed that drift-bottle returns reflect the passive dispersal of veligers, then a simple calculation can be made as before to show the likelihood that some larvae from each individual female will be returned to their parent population. A species such as *Cymatium nicobaricum* (Röding, 1798), estimated to spawn more than 500,000 eggs per female (Govan, 1994: 54), even with only 0.1% survival

Table 2. Drift bottles released in a quadrangle bounded by 18° to 23° N and 154° to 161° W in 1962 and subsequently recovered on islands of the Hawaiian Archipelago (data from Barclay *et al.*, 1964).

Time of year	No. of release points*	Total no. bottles released	Percent of bottles recovered
Jan. - Feb.	180	1005	2.7
March - May	59	925	12.5
June - July	182	1840	3.5
Sept. - Dec.	-	200	6.0

* From March through May returns were received from 52.5% of release points. During other parts of the year returns were received from only 9-11% of release points.

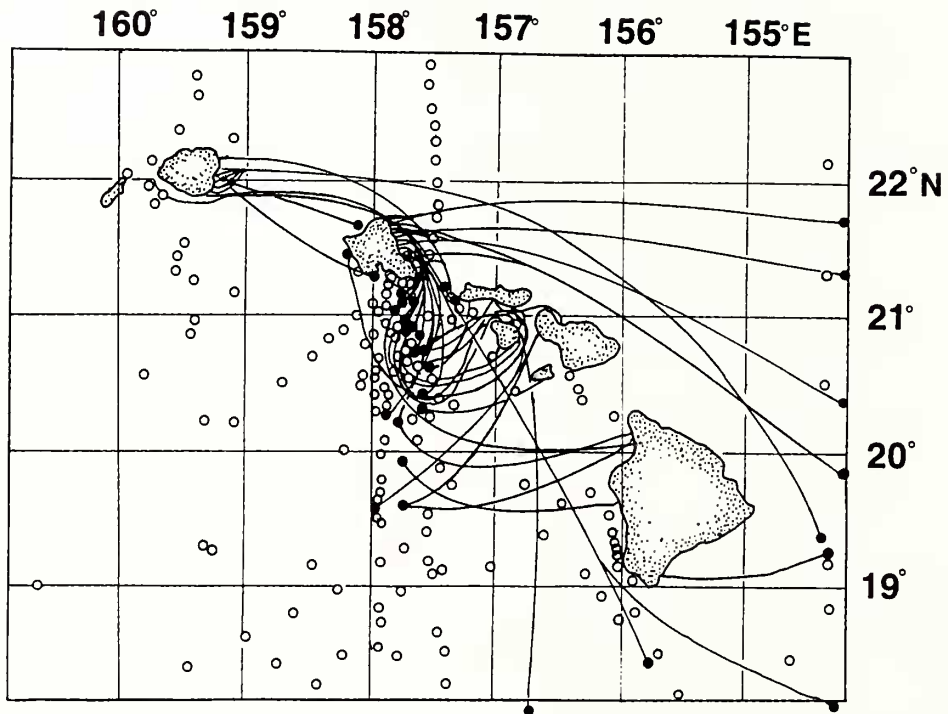


Fig. 6. Drift bottles released and recovered between January and June, 1962 (the time of highest returns), in a region bounded by 18° and 23° N and 154° and 161° W (modified after Barkley *et al.*, 1964: fig. 4-7). See also Table 2. Closed circles (●) indicate points of release from which returns were received; lines show probable route of drift bottles from point of release to location of recovery; open circles (O) show points of release from which no returns were received.

can reasonably be expected to have surviving offspring if 5.5% are returned to their parent island. On average most species found on oceanic islands by such calculations will be able to sustain an indigenous population.

CONCLUSIONS

There is much speculation in the foregoing account; obviously there remains much to be done, *e. g.* genetic studies using molecular techniques could support or refute some of the conclusions made here. One, nevertheless, must marvel at the remarkable means by which some larvae are apparently retained to sustain their parent population while others evidently are transported out to sea to colonize or to provide genetic continuity with other remote islands, and that both the dispersal and retention of larvae can be governed by the rotation and movement of mesoscale eddies.

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